Diversity and Abundance of Tropical American Scallops (Bivalvia: Pectinidae) from Opposite Sides of the Central American Isthmus

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Abstract. There is confusion about the comparative diversity of mollusks on opposite sides of the Isthmus of Panama due to inadequate sampling and contrasting patterns of diversity for different molluscan taxa. We report here on the occurrence of scallops (Bivalvia: Pectinidae) from extensive new dredge sample collections from the Gulf of Panama and Gulf of Chiriqui in the Eastern Pacific and from the San Blas archipelago to the Cochinos Cays in the Gulf of Honduras in the southwestern Caribbean. The collections contain more than 8000 specimens of 33 species from 213 collections. These include 22 Caribbean species and 11 Eastern Pacific species. However, the average abundance of scallops per collection is much higher in the Eastern Pacific so that the average number of species per collection was similar in the two oceans. This discrepancy in abundance is the principal reason previous workers have erroneously concluded that species diversity is equal or even greater in the Eastern Pacific than the Caribbean. Numbers of scallop species at the seven different Caribbean localities sampled average about one and one half times higher than the two regions in the Eastern Pacific, and the total differences in species richness are two times higher for all the regions combined. Most scallop species were common to abundant and scallop species do not exhibit a log series or log normal pattern of relative abundance. However, we found eight previously undescribed species, two in the Eastern Pacific and six in the Caribbean. These appear to be geminate species and are indistinguishable, pending detailed morphological study, from species occurring in the opposite ocean. These new species are all rare but typically occurred in sufficient abundance and at numerous localities so that their occurrence is not in question.

INTRODUCTION

The rise of the lower Central American Isthmus divided the once continuous tropical American ocean into two very different realms (Birkeland, 1977, 1987; Coates et al., 1996; D'Croz and Robertson, 1997; Jackson & D'Croz, 1998). Formation of the Isthmus occurred over about 20 million years (Coates et al., 2003) and the final separation of the oceans around 3.5 to 3.0 million years ago (Coates & Obando, 1996). Coastal environments on the two sides of the Isthmus are very different (Birkeland, 1977, 1987; Jackson & D'Croz, 1998). The tropical Eastern Pacific exhibits strong seasonal and inter-annual fluctuations in temperature and primary production associated with upwelling and El Niño events. Primary productivity of phytoplankton is great but coral reefs are poorly developed and seagrasses absent. In contrast, the tropical Western Atlantic exhibits much smaller seasonal and inter-annual variability, low planktonic productivity, and extensive development of coral reefs and seagrass meadows.

The isolation of the oceans also resulted in widely diverging patterns of evolution and taxonomic diversity among major taxa that were formerly quite similar across the developing Isthmus (Vermeij, 1978, 1993; Lessios,

1990; Jackson et al., 1993, 1996; Knowlton et al., 1993; Knowlton and Weight, 1998; Budd, 2000). Numbers of species of reef corals (Veron, 2000), cheilostome bryozoans (Cheetham & Jackson, 2000), and benthic foraminifera (Buzas & Culver, 1991; Collins, 1999) are considerably greater in the Western Atlantic than the Eastern Pacific, whereas crustaceans (Jones & Hasson, 1985) and echinoderms (Chesher, 1972) differ little across the Isthmus.

The diversity patterns for mollusks have been the subject of much confusion and debate because of great differences in sampling effort and taxonomic study. Woodring (1966) and subsequently others (Stanley & Campbell, 1981; Vermeij & Petuch, 1986; Petuch, 1995) concluded that the Western Atlantic fauna had suffered high extinction during the Pliocene that reduced diversity compared to the Eastern Pacific. However, more recent studies demonstrate that high extinction was balanced by high origination (Allmon et al., 1993, 1996; Jackson et al., 1993, 1999) and that the numbers of species in the two oceans are approximately the same (Roy et al., 2000).

In contrast, the diversity patterns of lower taxonomic levels exhibit great variation across the Isthmus. For example, gastropods of the *Strombina* Group have much higher diversity in the Eastern Pacific than the Western

Table 1

Previous studies covering the Caribbean, Gulf of Mexico, and Eastern Pacific regions.

Pacific studies	Taxa
Grau, 1959	9
Olsson, 1961	9
Keen, 1971	9
Previously described species	9
This study	11
Caribbean studies	Taxa
Olsson and McGinty, 1958	5
Abott, 1958	7
Bayer et al., 1970	15
Waller, 1973	18
Vokes and Vokes, 1983	12
Rios, 1985	10
Cahill, 1990	15
Merlano and Hegedus, 1994	16
Abbott and Morris, 1995	13
Mikkelsen and Bieler, 2000	22
Redfern, 2001	11
Previously described species	25
This study	25

Atlantic (Jung, 1989; Jackson et al., 1993, 1996; Fortunato, 1998). Similarly, the bivalve genus *Chione* is approximately twice as diverse in the eastern Pacific (Roopnarine, 2001). In contrast, the scallops in the Family Pectinidae are more diverse in the Western Atlantic (Table 1).

Mollusks of the tropical Eastern Pacific have been sampled more extensively than tropical Western Atlantic mollusks. There are no major compendia of the tropical Western Atlantic fauna comparable to those for the tropical Eastern Pacific (e.g., Grau, 1959; Olson, 1961; Keen, 1971; Coan et al., 2000); although numerous studies document the faunas of more limited areas such as the Bahamas (Redfern, 2001), Bermuda (Waller, 1973), Brazil (Rios, 1985), Colombia (Merlano & Hegedus, 1994), Florida Keys (Mikkelsen & Bieler, 2000), Jamaica (Humfrey, 1975), Panama (Olsson & McGinty, 1958; Radwin, 1969; Bayer et al., 1970), Cuba (Espinosa et al., 1994), and the Yucatan Peninsula (Ekdale, 1974; Vokes & Vokes, 1983).

Recent tropical Eastern Pacific scallops have been described in three monographs (Grau, 1959; Keen, 1971; Olsson, 1961) each of which described all nine known species. In contrast, the Family as a whole has not been fully documented in any one study for the Western Atlantic although different genera have been described in detail including *Argopecten* (Waller, 1969), *Nodipecten* (Smith, 1991), and the "chlamid" genera *Caribachlamys*, *Laevichlamys*, and *Spathochlamys* (Waller, 1993). Twenty-five species of scallops have been described from the tropical Western Atlantic but no one published report in-

cludes all the species and the average number of species per paper is 13. The highest reported diversity in one region is 22 from the Florida Keys (Mikkelsen & Bieler, 2000), and this was a compilation based on museum collections, private collections, and publications.

Here we describe the diversity and abundance of scallops from opposite sides of the Central American Isthmus obtained by extensive dredging along the Pacific coast of Panama and the Caribbean coast of Panama, Nicaragua, and Honduras. The very large numbers of samples and specimens allowed us to evaluate possible effects of sampling bias and to describe patterns of species diversity and relative abundance with confidence.

MATERIALS AND METHODS

All samples were obtained by Helena Fortunato from 1995 to 1998 as part of the Panama Paleontology Project using a bottom dredge and the research vessel *RV Urraca* of the Smithsonian Tropical Research Institute. The dredges were built at STRI and ranged in size from 27 to 29 inches in width, 17 to 27 inches in height, trailing a net with 1 inch mesh. The dredges were towed for 5 to 20 minutes depending on bottom conditions and depth and were usually brought up clogged and full of sediment. The 79 samples from the Eastern Pacific were obtained from depths of 6 to 380 meters depth and the 150 Caribbean samples from 7 to 538 meters. However, most of the samples from both oceans were from less than 100 meters depth. The geographic locations of all the samples are shown in Figure 1 and the details of locations, depth, and bottom characteristics for all the samples can be found at the PPP website (http://www.fiu.edu/~collinsl/index.html).

The samples were washed and sieved on deck using 8 mm and 2 mm mesh. Samples were sorted at STRI and all bivalves identified to genus or subgenus before shipment to the Scripps Institution of Oceanography. All scallops were identified to species by the first author.

Additional material examined for taxonomic reference included scallops from the Gibson-Smith collections of Venezuelan mollusks now housed at the Naturhistorisches Museum in Basel Switzerland (NMB), and from the first author's collections from deposits in the Enriquillo Valley in southwestern Dominican Republic and Bocas del Toro, Panama. Material from these additional collections was not used in analyses of diversity and abundance.

Diversity was measured as the number of species (richness), the Shannon-Weiner index of diversity H, calculated as $H = -\Sigma\ p_i \log p_i$, and Fisher's Alpha ($\alpha$) as N/S = $(e^{S/\alpha} - 1)/(S/\alpha)$. The latter is a best-fit solution for α. Both metrics were calculated using the STATPOD package for the statistics software R (Johnson & McCormick, 1999).

TAXONOMY AND SYSTEMATICS

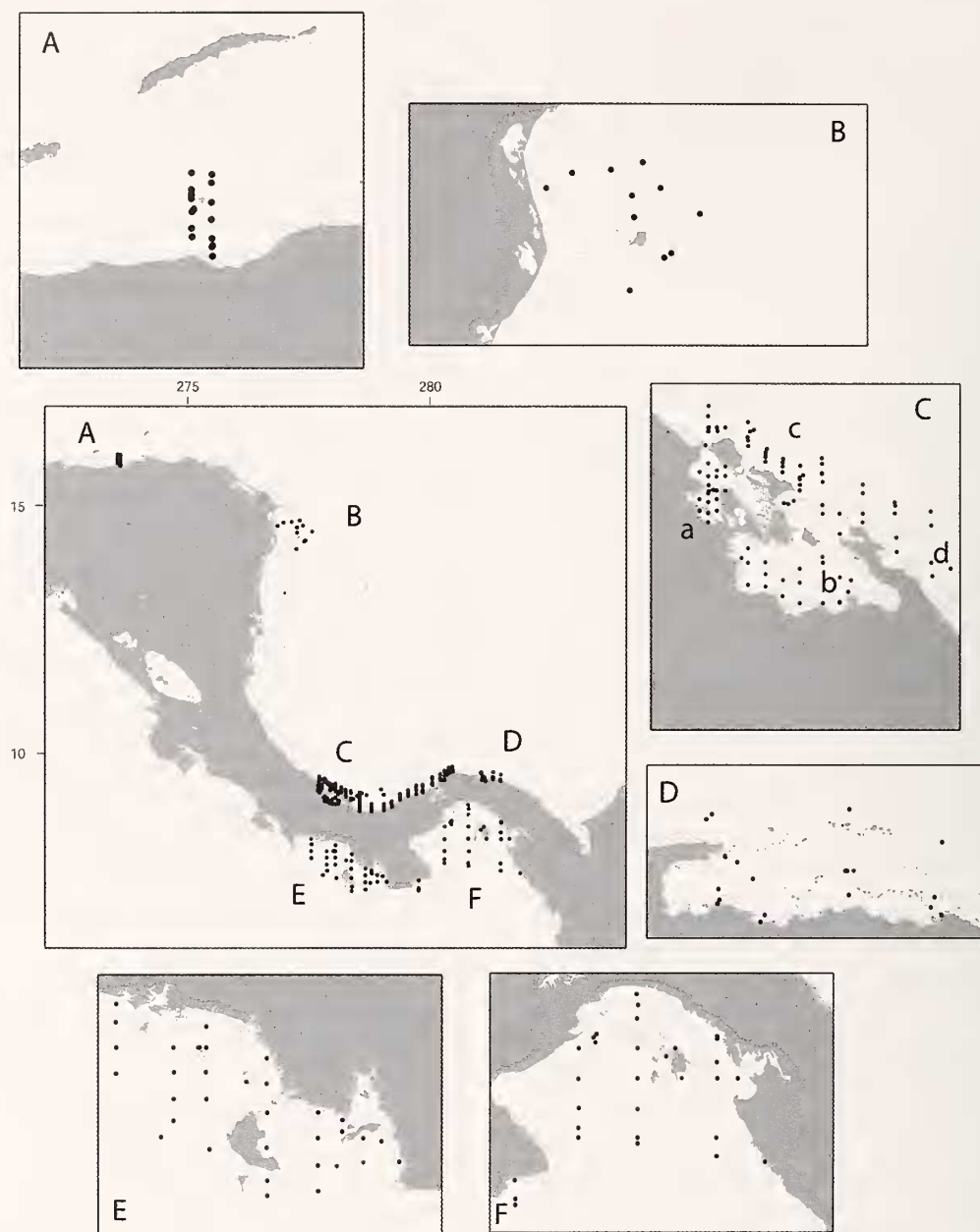Our goal was to describe patterns of species occurrences and abundance across the Isthmus without attempting

Figure 1. Locality maps. Central map shows the geographic locations of the localities used in this study. Surrounding maps show regional localities for (A) Cochinos Cays, Honduras, (B) Mosquito Cays, Nicaragua, (C) Bocas del Toro, Panama, (D) San Blas, Panama, (E) Gulf of Chiriqui, Panama, and (F) Gulf of Panama, Panama. Small letters on the Bocas del Toro map (C) depict the regions used in the study. These are (a) Almirante Bay, (b) Chiriqui Lagoon, (c) Bocas del Toro, and (d) Gulf of Mosquitoes.

any systematic revision of higher taxonomic categories that would be inappropriate without thorough examination of material from outside the region of study. In general, we followed the systematic framework of Waller (1969, 1986, 1991, 1993) that has received strong support from independent molecular genetic data based on mitochondrial cytochrome c oxidase CO1 (Matsumoto & Hayami, 2000) and mitochondrial 16s and 12S rRNA

genes (Barucca et al., 2004). Additional sources for taxa not covered in Waller's work include Grau (1959), Olsson (1961), Keen (1971), Moore (1984), Rios (1985), Smith (1991), Abbott and Morris (1995), and Coan et al. (2000).

We did not subdivide genera into subgenera because of inconsistent usage in the literature, and because species within the different genera could be consistently and un-

ambiguously distinguished on the basis of one or more characters regardless of their subgeneric classification. The only exception is *Pseudamussium* (*Peplum*) as traditionally used for the species *P.* (*P.*) *fasciculatum* (Hinds, 1845) (Figures 2I, J, M, N). *Nodipecten* has been considered both a subgenus of *Lyropecten* (Keen, 1971; Jackson et al., 1999) and as a separate genus (Smith, 1991; Abbott & Morris, 1995; Coan et al., 2000). *Nodipecten* can be separated from species of *Lyropecten* based on the ribbing pattern (Smith, 1991). Members of the genus *Lyropecten* have a left valve ribbing pattern of r-RrrRcrrRr or rNrrNcrrNr where r represents a rib, R a key or more pronounced rib, N represents a key rib with nodes, and Nc signifies the central, noded rib following Smith (1991). In *Nodipecten* this arrangement is rRr-RcrRr or rNrNcrNr. The species *Nodipecten arthriticus* (Reeve, 1853) (Figures 3D, E) and *Nodipecten* sp. G (Figure 3C) are problematic in that they have the ribbing pattern rNrrNcrNr, which is intermediate to the characteristics of *Lyropecten* and *Nodipecten*. However, pending systematic revision, we have placed species with this ribbing pattern in the genus *Nodipecten* following Smith (1991) and Coan et al. (2000).

Pacipecten has been considered as a subgenus of both *Leptopecten* (Keen, 1971) and *Aequipecten* (Olsson 1961), and as a separate genus (Moore, 1984). Olsson (1961) originally described *Pacipecten* as a subgenus of *Aequipecten*. Later workers have gone back and forth treating the group as a subgenus or a genus. Species of *Pacipecten* and *Leptopecten* appear to form a clade and can be consistently separated from other groups based on their hinge morphology. In both genera there are two pairs of hinge teeth on the right valve and the anterior resilial tooth is the dominant tooth (Figure 4A). The genus *Pacipecten* can be separated from *Leptopecten* by the very fine or absent concentric lirae, making the shell appear almost smooth, and the absence of secondary or tertiary ribbing (Figure 5C). In the genus *Leptopecten* the concentric lirae are strong, often creating a flange-like appearance, and secondary or tertiary ribs are present in all of the tropical American species, although not in a consistent manner (Figure 5A, B).

The genus *Euvola* is the most problematic. Waller (1991) combined the living tropical American species previously assigned to the genera *Oppenheimopecten*, *Flabellipecten*, and *Amusium* into the genus *Euvola* based on observations that the species in question share certain morphological traits, and are quite certainly not members of the genera to which they have traditionally been assigned. While there are morphologic characters that apparently separate the species herein assigned to this genus into identifiable groups, the systematic approach of Waller has been followed here pending further work.

We used open nomenclature for the species Pectinid A *lineolaris* (Lamarck, 1819) (Figure 6A, B). This species

has most recently been assigned to the genus *Argopecten* (Waller, 1969, 1991). The morphology of the hinge teeth indicates a close relationship with this genus. However, the early dissoconch microstructure of the left valve is unique to this species among those observed in these collections. In members of the genus *Argopecten*, as in all of those genera in the "*Aequipecten*" group observed in this study—*Lindapecten*, *Pacipecten*, and *Leptopecten*— a microstructure consisting of coarse pitting begins very early in the early dissoconch stage (Figure 7A, B). In Pectinid A the onset of this structure is delayed or extremely reduced (Figure 7C, D). In this case, as in the genera discussed above, the generic placement is not crucial to the analyses presented here. The diversity and rarity data presented are all based on species level identifications and are not examined at the genus level.

Species were identified using easily observed morphologic characters. Examples of all species identified and used in the analyses presented here are illustrated in Figures 2, 3, 6, 9–13. These figures also include several specimens that were used for comparison with observed species. The most readily observed character is valve symmetry. Species traditionally placed in the subfamily Pectininae have highly asymmetrical valves. The left (upper) valve is generally flat or even concave and the right (lower) valve is convex (Figure 8C, D). In all other species in the family, the valves are equal to sub-equal in convexity (Figure 8A, B). However, recent molecular work has questioned of the validity of this character for defining sub-familial groups within the Pectinidae (Frischer et al., 1998; Canapa et al., 2000; Steiner & Muller, 1996; Barucca et al., 2003). This apparent disconnect between traditional, easily observed morphologic characters and phylogenetic relationships based on molecular data is the primary reason for our decision to analyze diversity only at the species level pending further systematic work on the group to sort out higher level taxonomic relationships.

Hinge teeth are also an important taxonomic character as discussed above in regards to *Pacipecten* and *Leptopecten*. Waller (1986, 1991) presented a consistent identification and nomenclatural scheme for pecten hinge teeth, also called crura. The primary morphologic differences in hinge teeth relate to number of pairs and dominance of the teeth, illustrated in Figure 4, which differs depending on the left and right valves of the taxon in question. The remaining characters used for identification of species are rib count, presence or absence of secondary or tertiary ribbing, presence and strength of concentric lirae, and pattern of rib dominance and ribs with nodes.

In this study we have identified several taxa that are heretofore undescribed and are designated informally as species A, B, etc. In all but two cases these taxa are similar to species known from the opposite ocean and
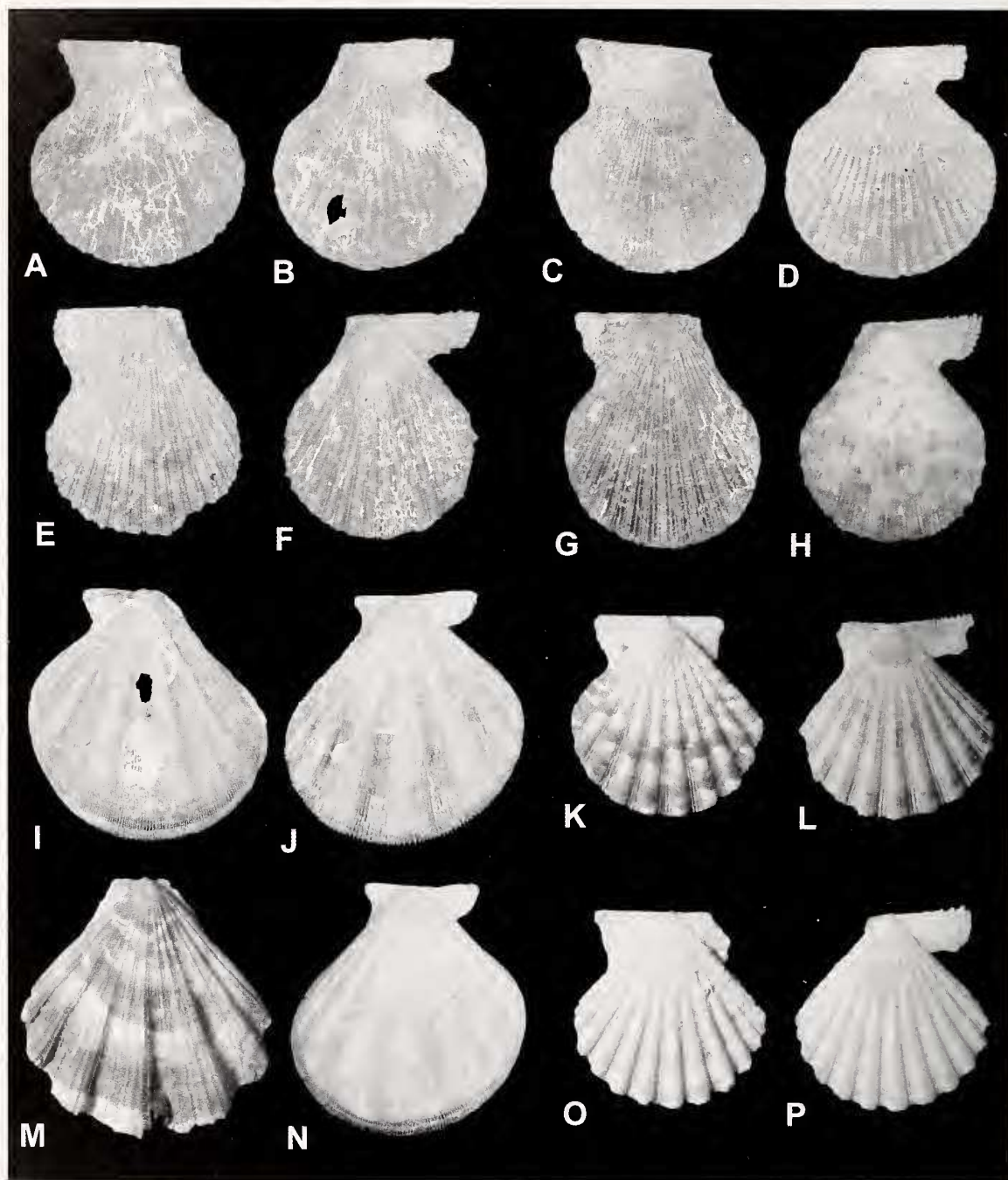
Figure 2. *Spathochlamys, Pseudamussium (Peplum)*, and *Bractechlamys*. (A) *Spathochlamys benedicti* (CTPA 540-B-52, lvh = 14.15 mm), (B) *S. benedicti* (CTPA 493-B-124, rvh = 15.79 mm), (C, D) *S. cf. vaginula* (jts 06-B-11, (C) lvh = 16.27 mm, (D) rvh = 13.13 mm), (E, F) *S. vestalis* (CTPA 399-B-146, (E) lvh = 12.36 mm, (F) rvh = 13.13 mm), (G, H) *S.* sp. A (CTPA 538-B-101, (G) lvh = 14.79 mm, (H) rvh = 14.08 mm), (I, J) *Pseudamussium (Peplum) fasciculatum* (CTPA 415-B-72, (I) lvh = 29.81 mm, (J) rvh = 28.15 mm), (K, L) *Bractechlamys antillarum* (CTPA 431-B-72, (K) lvh = 16.35 mm, (L) rvh = 18.55 mm), (M) *P. (P.)* sp. D (CTPA 525-B69, lvh = 18.87 mm), (N) *P. (P.)* sp. D (CTPA 338-B-85, rvh = 28.0 mm), (O) *B.* sp. H (CTPA 362-B-1, lvh = 14.09 mm), (P) *B.* sp. H (CTPA 412-B-1, rvh = 14.04 mm).
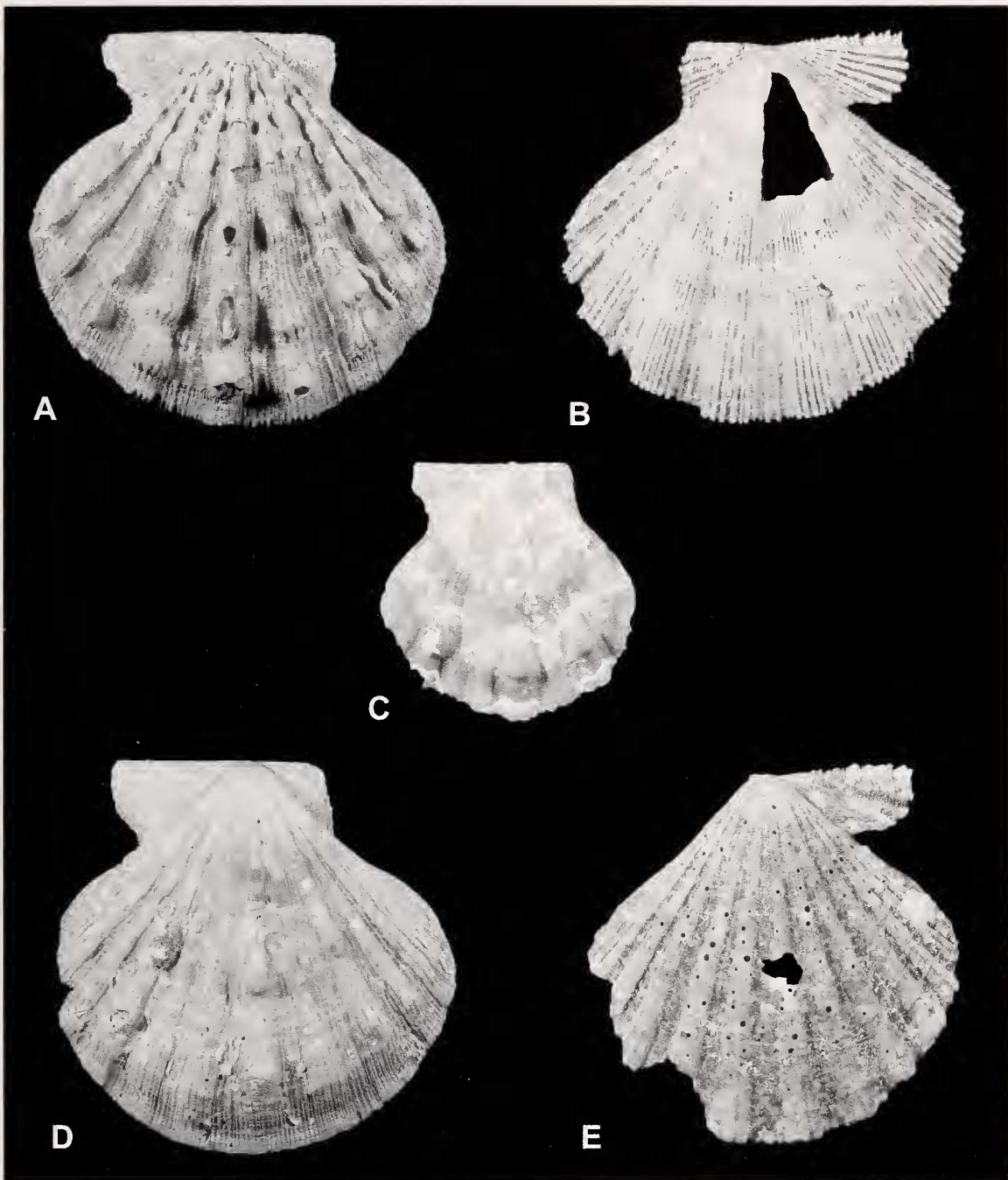
Figure 3. *Nodipecten.* (A) *Nodipecten nodosus* (jts 06.13-B-13, lvh = 85.75 mm), (B) *N. nodosus* (CTPA 403-B-84, rvh = 66.81 mm), (C) *N.* sp. G. (CTPA 494-B-57, lvh = 15.36 mm), (D) *N. arthriticus* (CTPA 403-B-45, lvh = 97.37 mm), (E) *N. arthriticus* (CTPA 389-B-84, rvh = 53.05 mm).

may be geminate species pairs. The two undescribed species that are not considered geminate species are *Euvola* sp. cf. *E. raveneli* (Dall, 1898) (Figure 9F), which is represented by very few identifiable specimens, and *Caribachlamys* sp. cf. *C. mildredae* (Bayer, 1941) (Figure

10A, B). The latter species was found by the first author while snorkeling in Bocas del Toro but not in any of the dredge samples, and is therefore not included in the analyses of diversity. A final species, tentatively identified as *Euvola* cf. *laurenti* (Gmelin, 1791), was not included in
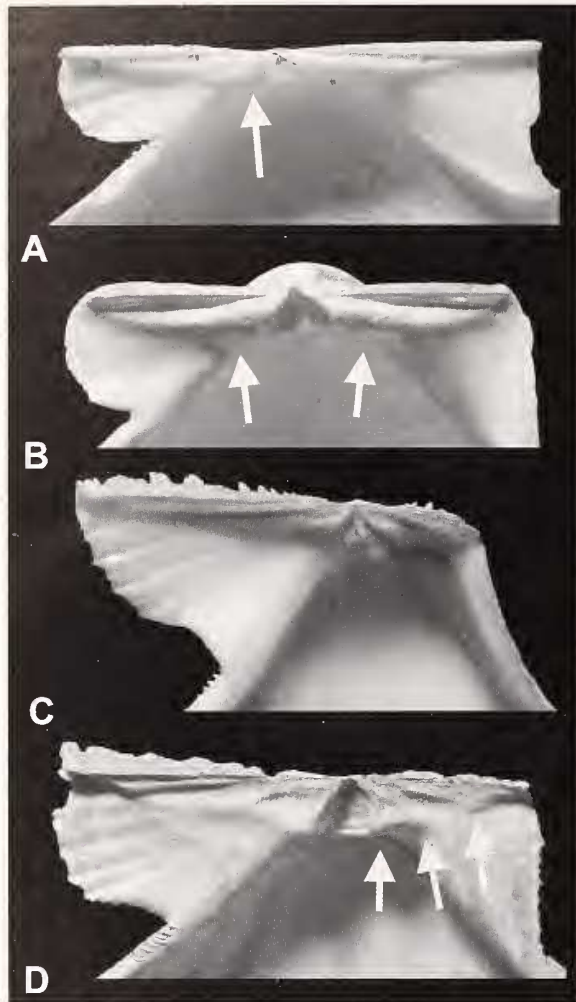
Figure 4. Illustration of the described hinge morphologies. Two pairs of hinge teeth with the anterior resilial tooth dominant (A). Two pairs of hinge teeth with the resilial teeth dominant and extended (B). Two pairs of hinge teeth with no dominant teeth (C). More than two pairs (3 in this case) of hinge teeth (D). Specimens shown are (A) *Pacipecten tumbezensis* (CTPA 381-B-70, hl = 25.54 mm), (B) *Argopecten gibbus* (NMB 17662, hl = 31.52), (C) *Caribachlamys* cf. *mildredae* (jts 11-B-1, hl = 14.32), and (D) *Nodipecten nodosus* (NMB G 17477, hl = 64.34). Terminology follows Waller (1986, 1991, 1993).

this study because it occurred as a single fragment from one sample in the Eastern Pacific.

PATTERNS OF SPECIES DIVERSITY

We obtained 3915 specimens of 11 species of scallops in 74 samples from the Eastern Pacific and 4434 specimens of 22 species in 139 samples from the Caribbean (Table 2). The number of living specimens was less than 0.1% of the total, so these results are based on time-averaged assemblages representing hundreds to thousands of years (Kidwell, 2002a). Death assemblages have been shown
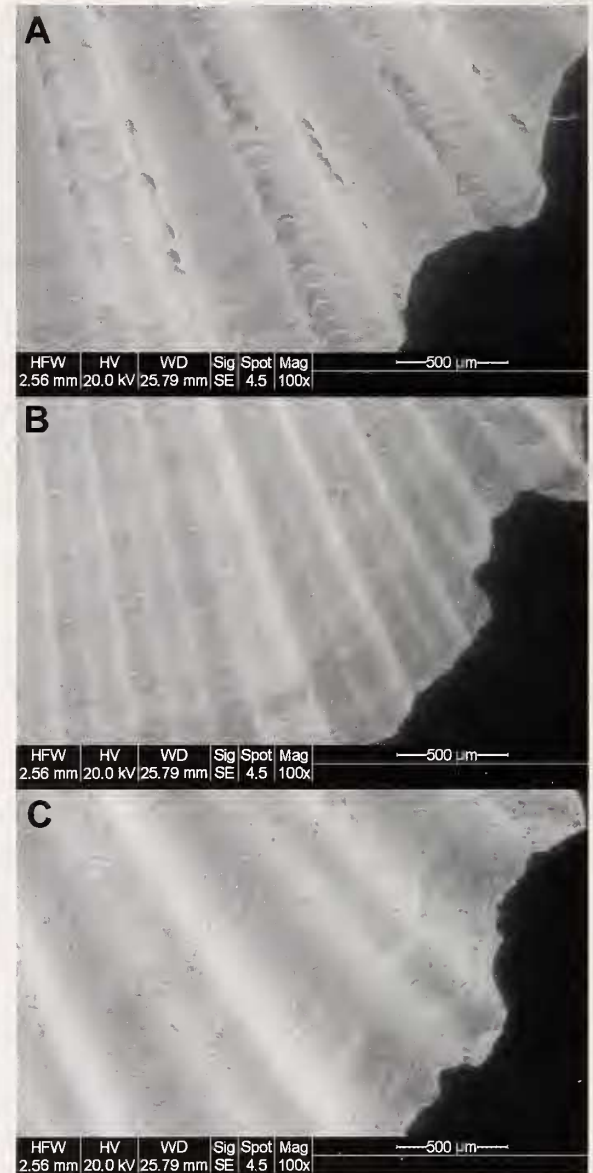

Figure 5. Shell morphology of *Leptopecten* and *Pacipecten*. The characteristics of *Leptopecten* (A, B) are strong concentric lamellae and the presence, in most taxa, of secondary ribbing, and in *Pacipecten* (C) are very fine concentric lamellae and absence of secondary or tertiary ribbing. Specimens shown are (A) *Leptopecten biolleyi* (CTPA 387-B-151), (B) *Leptopecten bavayi* (CTPA 577-B-34), and (C) *Pacipecten linki* (CTPA 458-B-100).

to faithfully represent the relative abundance of the local fauna (Kidwell, 2001, 2002a). This is particularly true when the focus is on larger mesh sizes (> 1.5 mm) as is the case in this study (Kidwell, 2002b). Collector's curves of numbers of species found as a function of numbers of specimens or samples level off well before all the samples are included so that the differences in diversity are robust (Figure 14). However, the abundance of specimens per
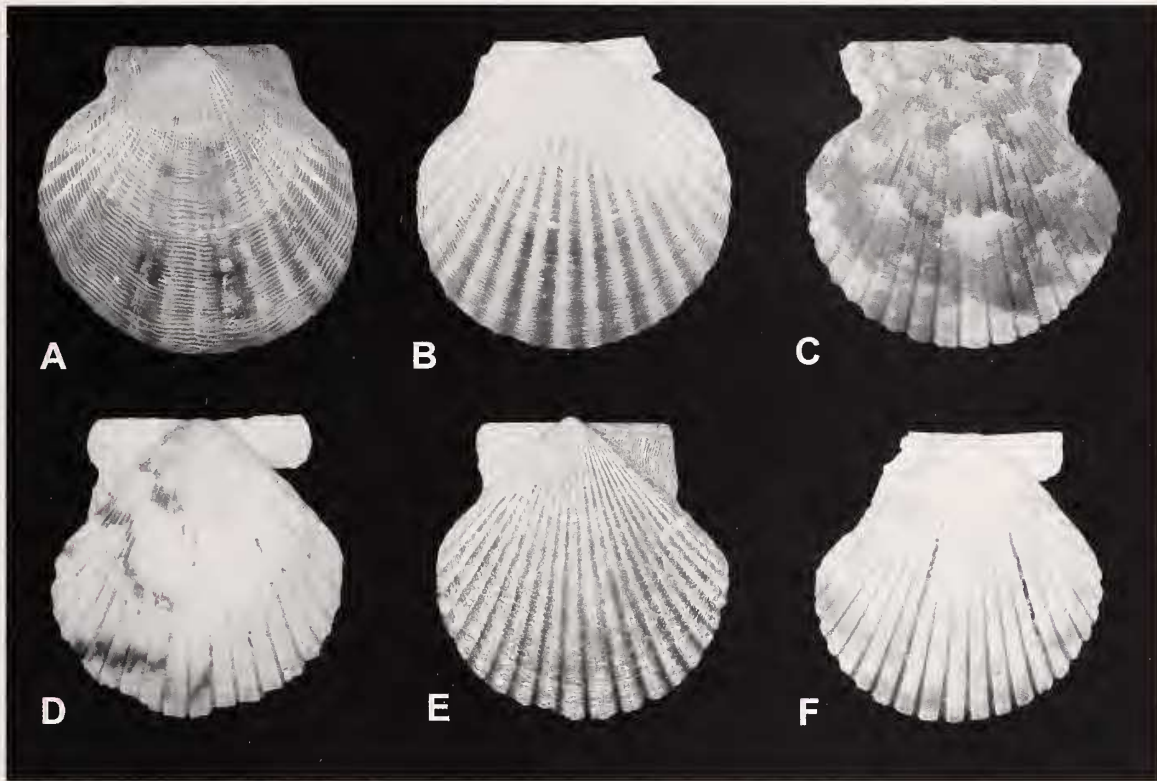
Figure 6. *Argopecten* and Pectinid A. (A, B) PectinidA *lineolaris* (NMB G 17478, both valves height = 39.69 mm), (C) *Argopecten gibbus* (CTPA 326-B-25, lvh = 19.57 mm), (D) *A. gibbus* (CTPA 336-B-47, rvh = 15.72 mm), (E, F) *A. ventricosus* (CTPA 399-B-27, (E) lvh = 16.70 mm, (F) rvh = 13.02 mm).

dredge sample was much greater in the Pacific collections (2 × 2 contingency table, chi square = 556.72, $P \ll$ 0.0001). Nearly twice the number of samples in the Caribbean yielded only 12% more specimens than were collected in the Pacific. There are two important consequences of these differences in abundance between the oceans. First, the average number of species per locality is about four in both oceans, despite the much greater overall diversity in the Caribbean (Figure 15A). Second, the sampling curves are slightly flatter for the Eastern Pacific collections. More specimens per locality equate to higher local species richness and more complete sampling with lower effort.

In the Eastern Pacific, numbers of species were lower in the Gulf of Panama than the Gulf of Chiriqui (Table 3). There were only small differences in the Shannon-Weiner Index (H) and Fisher's Alpha (α) diversity measures between these two regions. Diversity in the Gulf of Chiriqui was slightly lower using H and slightly higher using α. We found all nine of the previously described species from the Eastern Pacific, although not always in both regions. The two additional species reported here are undescribed and are apparently geminate species (Table 4). *Lindapecten* sp. B (Figure 11C, D) was found in both the Gulf of Panama and Gulf of Chiriqui, but *Bractech-lamys* sp. H (Figure 2O, P), was found only in the Gulf of Chiriqui. *Lindapecten* sp. B is virtually indistinguishable from *L. acanthodes* (Dall, 1925) (11A, B) in the Caribbean as is *Bractechlamys* sp. H from *B. antillarum* (Recluz, 1853) (Figure 2K, L) in the Caribbean. Both species were identified from well-preserved complete specimens collected at multiple localities (Table 2).

Sampling completeness was not as good in the Caribbean as in the Eastern Pacific. All of the Caribbean regions except Bocas del Toro contained only two thirds or less of the total Caribbean species collected. Species richness ranged from 14 to 17 species for all the regions except Bocas del Toro (Table 3), and sampling curves were indistinguishable except for the latter region. The Shannon-Weiner Index (H) is highest (H > 1.9) in the Bocas del Toro, San Blas, Almirante Bay, and Cochinos Cays regions. H was lowest (H < 1.8) in the Mosquito Cays, Gulf of Mosquitoes, and Chiriqui Lagoon regions. There is very little difference among these groups. Fisher's Alpha (α) was highest (α > 3.6) in the Bocas del Toro, Gulf of Mosquitoes, and Los Cochinos regions. Alpha was lowest (α < 3.1) in the Chiriqui Lagoon, Mosquito Cays, and Almirante Bay regions. The San Blas region was intermediate between these groupings.

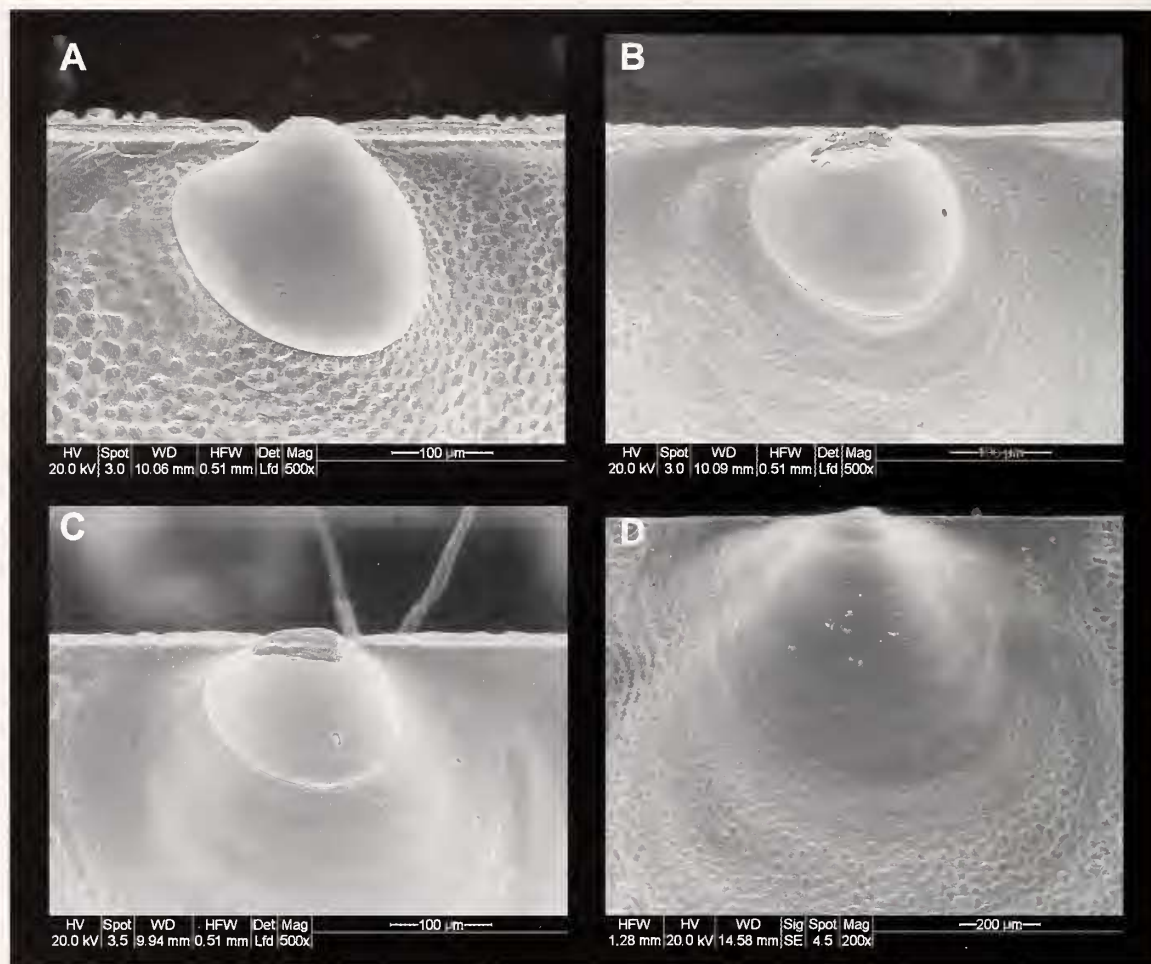We found 6 new species in the Caribbean samples, all

Figure 7. Left valve early dissoconch microstructure. *Aequipecten* like structure (A, B) showing early origination of pitted microsculpture and (C, D) the modified form seen on specimens assigned herein to the genus Pectinid A showing delayed onset of pitted microsculpture. Specimens shown are (A) *Leptopecten biolleyi* (CTPA 373-B-89), (B) *Argopecten gibbus* (CTPA 482-B-15) and (C and D) Pectinid A *lineolaris* (CTPA 519-B-106-1 and 519-B-106-2).

of which were rare. All of these undescribed species appear to be geminate sister species to taxa in the Eastern Pacific (Table 4) and are so far indistinguishable morphologically based on the small numbers of specimens available. An additional species, represented by 15 left valves, may be *Euvola raveneli* but due to the lack of right valve specimens we are considering it *Euvola* sp. cf. E. raveneli. No specimens of *E. raveneli* were positively identified in the collections.

COMMONNESS and RARITY

The tropical American scallops do not fit a typical log series or log normal pattern of relative abundance (Figure 15A) observed for mollusks as a whole (Buzas et al., 1982), but more closely resemble abundance patterns of free-living bryozoans from the same region (Cheetham & Jackson, 2000). Most of the species are common to abun-

dant and there are fewer rare species compared to other groups. Five out of the 11 Eastern Pacific species (45%) were found in more than 20% of the samples whereas only 7 of the 21 Caribbean species (33%) occurred as frequently (Figure 15B). Despite the poor statistical fit to a log normal distribution, we can perform the exercise of estimating the effect additional sampling would have for discovering additional species in the two oceans (Buzas et al., 1982). In the eastern Pacific a doubling of sampling effort would be assumed to produce roughly 1 or 2 more species. In the Caribbean this number is a little higher, between 2 and 3. In fact, we know that our collections do not contain 5 species of scallop that are described from the Caribbean and the Gulf of Mexico.

Rabinowitz (1981) defined rarity in terms of geographic range and abundance (see also Gaston, 1994). We plotted the proportion of localities in which the species occurs
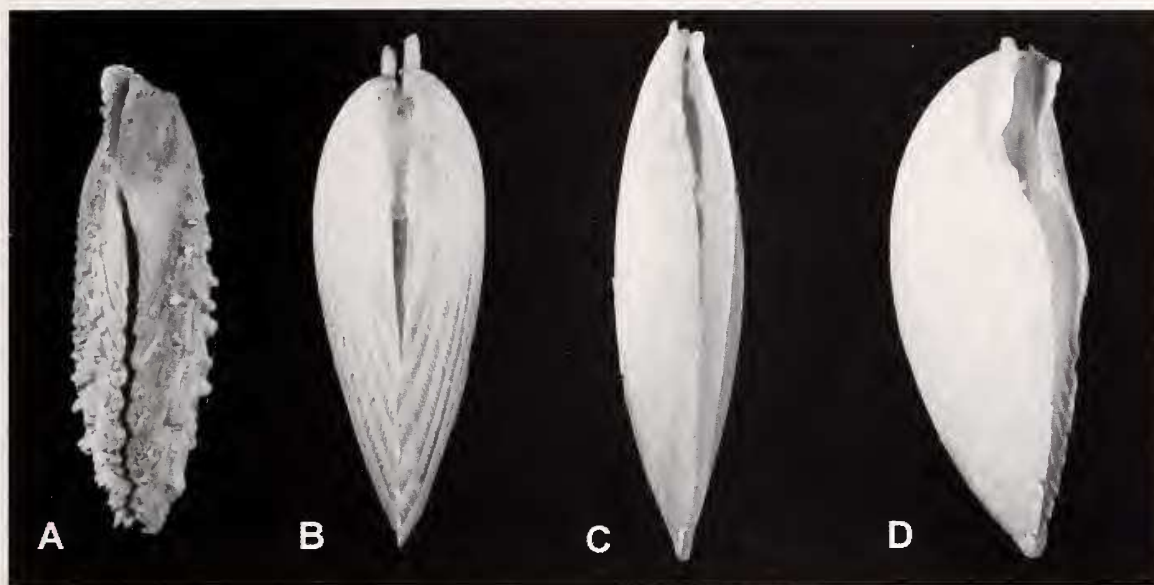
Figure 8. Shell symmetry. Illustration of the common forms of shell convexity in scallops. Equal to sub-equal convexity (A and B) and unequal to highly unequal convexity (C and D). Specimens shown are (A) *Caribachlamys* cf. *mildredae* (jts 11-B-1, height (ht) = 26.44 mm), (B) Pectinid A *lineolaris* (NMB G 17478, ht = 39.69 mm), (C) *Euvola marensis* (NMB G 17479, ht = 59.92 mm), and (D) *Euvola ziczac* (NMB G 17480, ht = 49.05 mm).

against the log of abundance for each species in the samples (Figure 16). We then divided the field into 4 quadrants defined by the median values of the two axes; high abundance and wide range (upper right), low abundance and wide range (upper left), high abundance and small range (lower right), and low abundance and small range (lower left). Abundance and frequency of occurrence are highly positively correlated as has been commonly observed for other taxa (Jackson, 1974; Cheetham & Jackson, 1996). In both oceans, 45% of the species occur in the upper right quadrant of this plot. Four of the five most frequently occurring species are from the Pacific (squares in Figure 16) whereas the four species found at the lowest percentage of localities are all from the Caribbean (circles in Figure 16). In addition, 7 of the 8 previously undescribed species (solid points) are in the lower left (fewest localities and lowest abundance) quadrant. The eighth species is relatively abundant but not widespread.

DISCUSSION

The problems associated with sampling rare species can have a strong effect on taxonomic practice as revealed by the rare species recorded in this study. First, all of the 8 previously undescribed species are virtually identical to previously described species in the other ocean and are likely geminate species (Table 4). Most of these species are rare. Very similar results were observed for gastropods of the *Strombina* group, for which the numbers of apparent geminate species pairs increased substantially

with increased sampling (compare Jung, 1989 with Jackson et al., 1993, 1996). The rarity of one or the other of geminate species pairs likely reflects response to changing environmental conditions since the final separation of the two oceans by the rising Isthmus of Panama.

Second, the rarity of apparent geminate species may sometimes result in the failure to record an entire genus or subgenus from one ocean or the other. For example, the discovery of *Pseudamusium* (*Peplum*) sp. D cf. *P.* (*P.*) *fasciculatum* (Figure 2M, N) is the first reported occurrence of this genus or sub-genus in the Caribbean.

Third, the rarity of certain taxa may lead taxonomists to mistakenly question the provenance of apparently rogue specimens in old museum collections. For example, *Lindapecten* sp. B cf. *L. acanthodes* (Dall, 1925) in the Pacific and *Spathochlamys* sp. A cf. *S. vestalis* (Reeve, 1853) may actually have been previously described and later discredited due to lack of additional material. Grau (1959) discussed the species *Pecten squarrosus* Carpenter, 1865. Due to the similarity of the type specimen of *P. squarrosus* to *L. acanthodes* in the Caribbean, and the absence of any additional specimens resembling the type specimen in the Eastern Pacific, the name was considered *nomen dubium*. Grau did take into consideration known problems with Carpenter's localities. Our point here is not that this name is in fact valid, but that discrediting of the name based solely on the lack of subsequent material is questionable because so many species are rare.

The occurrence of the species *Spathochlamys* sp. A (Figure 2G, H) in the Caribbean is a similar example.
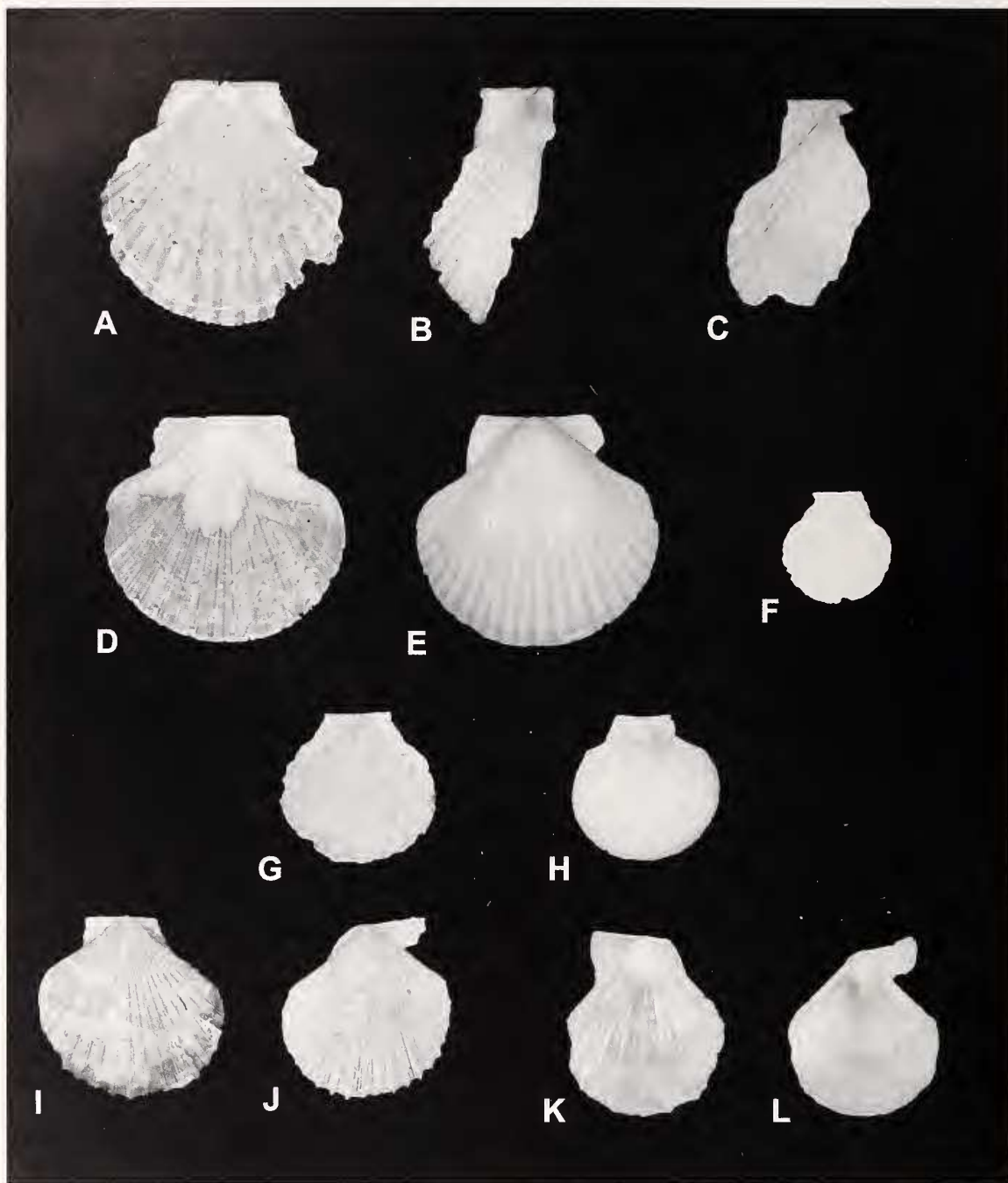
Figure 9. *Euvola, Cryptopecten,* and *Laevichlamys.* (A, B) *Euvola sericeus* (CTPA 405-B-25, (A) lvh = 43.64 mm, (B) rvh = 42.80 mm), (C) *E.* sp. E. (CTPA 326-B-52, rvh = 36.01 mm), (D, E) *E. ziczac* (NMB 17662-B-3, (D) lvh = 47.35 mm, (E) rvh = 49.05 mm), (F) *E.* cf. *raveneli* (CTPA 503-B-115, lvh = 12.4 mm), (G) *E. chazaliei* (CTPA 482-B-4, lvh = 20.05 mm), (H) *E. chazaliei* (CTPA 329-B-9, rvh = 22.8 mm), (I, J) *Cryptopecten phrygium* (NMB G 17481, (I) lvh = 31.58 mm, (J) rvh = 23.8 mm), (K, L) *Laevichlamys multisquamata* (CTPA 579-B-4, (K) lvh = 16.81 mm, (L) rvh = 12.25 mm).
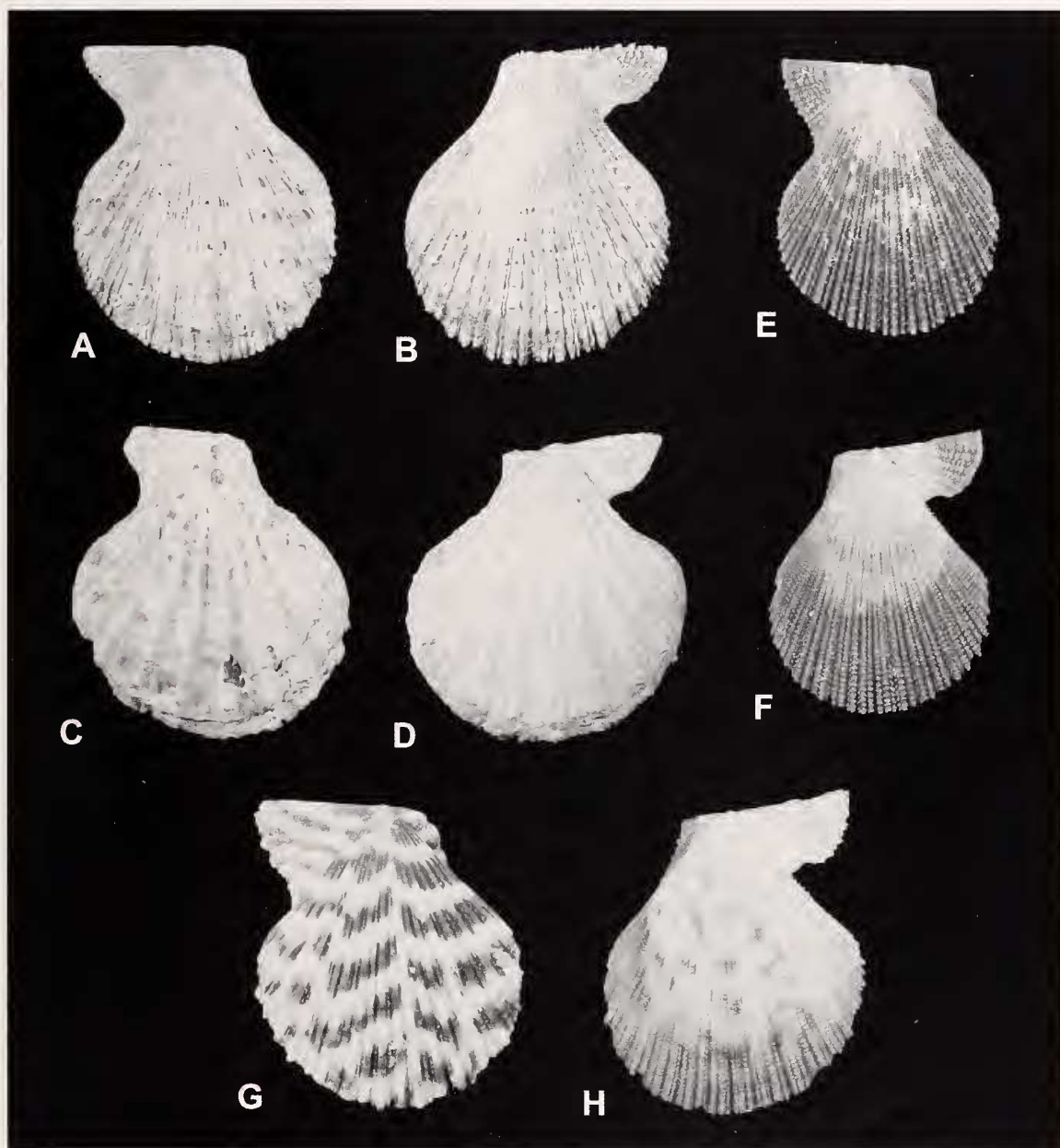
Figure 10.   *Caribachlamys.* (A, B) *Caribachlamys* cf. *mildredae* (jts 11-B-1, (A) lvh = 26.5 mm, (B) rvh = 26.58 mm), (C, D) *C. imbricata* (NMB G 17482, (C) lvh = 35.01 mm, (D) rvh = 34.75 mm), (E) *C. sentis* (CTPA 525-B-7, lvh = 13.67 mm), (F) *C. sentis* (CTPA 487-B-89, rvh = 13.66 mm), (G, H) *C. ornata* (NMB G 17483, (G) lvh = 18.39 mm, (H) rvh = 17.74 mm).

Spathochlamys vestalis (Figure 2E, F) was originally described from the West Indies. Waller (1993) determined this locality to be in error, partially based on the resemblance of the type specimen to specimens of *Chlamys lowei* (Hertlein, 1935) from the Gulf of California. Again, Waller did take into account known locality errors within Reeve's collection. However, the discovery of *Spathochlamys* sp. A in the Caribbean may in fact indicate that the original locality data was not in error. This would necessitate the use of the name *Spathochlamys vestalis* for the Caribbean species, and *Spathochlamys lowei* for the eastern Pacific species. We are not advocating this nomenclatural change in this paper, only again emphasizing the dangers associated with making assumptions regarding geographic distributions based on faunas that have not been sampled sufficiently.

A final similar example concerns *Caribachlamys* cf. *mildredae* (Figure 10A, B) that was recently collected by

Table 2

Occurrences of all species reported from the CTPA samples and used in this study. The occurrences are reported as number of localities/number of specimens. The second column (Figure) refers to the figure number illustrating the specimen in this paper. Regions cited are (GC) Gulf of Chiriqui, Panama, (GP) Gulf of Panama, Panama, (LCH) Cochinos Cays, Honduras, (CMN) Mosquito Cays, Nicaragua, (BT) Bocas del Toro, Panama, (BA) Almirante Bay, Panama, (LC) Chriqui Lagoon, Panama, (GM) Gulf of Mosquitoes, Panama, and (SB) San Blas, Panama.

Taxa	Figure	GC	GP	LCH	CMN	BT	BA	LC	GM	SB	Total
Argopecten gibbus (Linnaeus, 1758)	6 c, d	—	—	12/86	10/251	3/3	3/4	3/9	—	15/50	46/403
Argopecten ventricosus (Sowerby II, 1842)	6 e, f	33/1087	25/196	—	—	—	—	—	—	—	58/1283
Bractechlamys antillarum (Recluz, 1853)	2 k, l	—	—	7/9	5/12	11/41	5/70	8/80	9/34	4/9	55/311
Bractechlamys sp. H	2 o, p	3/7	—	—	—	—	—	—	—	—	3/7
Caribachlamys imbricata (Gmelin, 1791)	10 c, d	—	—	3/3	1/1	5/8	2/2	3/6	—	1/1	17/33
Caribachlamys sentis (Reeve, 1853)	10 e, f	—	—	2/3	2/2	4/7	3/4	5/8	1/1	1/1	19/27
Euvola cf. raveneli (Dall, 1898)	9 f	—	—	1/1	—	4/9	2/4	—	—	1/1	8/15
Euvola chazaliei (Dautzenberg, 1900)	9 g, h	—	—	11/61	8/17	14/124	2/58	6/48	12/426	10/17	64/752
Euvola laurenti (Gmelin, 1791)	12 c, d	—	—	5/11	5/15	8/25	4/5	19/165	6/14	5/16	53/252
Euvola perulus (Olsson, 1961)	12 e, f	14/65	17/45	—	—	—	—	—	—	—	31/110
Euvola sericeus (Hinds, 1845)	9 a, b	4/22	1/1	—	—	—	—	—	—	—	5/23
Euvola sp. E	9 c	—	—	1/1	—	—	—	—	—	—	1/1
Euvola sp. F	12 g, h	—	—	—	—	4/10	1/2	1/1	4/8	—	10/21
Euvola ziczac (Linnaeus, 1758)	9 d, e	—	—	2/2	3/3	3/3	—	3/4	1/3	—	17/46
Laevichlamys multisquamata (Dunker, 1864)	9 k, l	—	—	3/5	3/3	3/5	5/7	—	5/20	1/1	12/31
Leptopecten bavayi (Reeve, 1852)	13 g, h	—	—	3/4	—	6/12	—	5/6	3/6	2/3	30/62
Leptopecten biolleyi (Hertlein and Strong, 1946)	13 a, b	29/1243	21/380	—	—	—	—	—	—	—	50/1623
Leptopecten sp. C	13 c, d	—	—	—	—	7/42	3/9	1/1	2/24	—	13/76
Leptopecten velero (Hertlein, 1935)	13 e, f	6/12	—	—	—	—	—	—	—	—	6/12
Lindapecten acanthodes (Dall, 1925)	11 a, b	—	—	14/30	10/65	6/59	3/33	8/18	5/48	9/15	62/379
Lindapecten sp. B	11 c, d	2/3	2/3	—	—	—	—	—	—	—	4/6
Nodipecten arthriticus (Reeve, 1853)	3 d, e	9/31	—	—	—	—	—	—	—	—	9/31
Nodipecten nodosus (Linnaeus, 1758)	3 a, b	—	—	4/4	6/6	1/2	—	—	1/1	8/10	24/49
Nodipecten sp. G	3 c	—	—	—	—	3/5	1/2	1/1	—	—	5/8
Pacipecten leucophaeus (Reeve, 1852)	13 k	—	—	—	—	2/2	—	—	—	—	2/2
Pacipecten linki (Dall, 1926)	13 l, m	—	—	1/3	3/5	6/49	3/7	8/19	4/36	2/2	27/121
Pacipecten tumbezensis (d'Orbigny, 1846)	13 i, j	28/487	23/126	—	—	—	—	—	—	—	51/613
Pectinid A lineolaris (Lamarck, 1819)	6 a, b	—	—	7/31	5/11	19/388	7/106	16/351	18/468	10/35	84/1416
Pseudamusium (Peplum) fasciculatum (Hinds, 1845)	2 i, j	7/35	2/5	—	—	—	—	—	—	—	9/40
Pseudamusium (Peplum) sp. D	2 m, n	—	—	1/1	2/2	2/2	—	2/5	2/3	—	9/13
Spathochlamys benedicti (Verrill and Bush, 1897)	2 a, b	—	—	10/27	6/15	14/101	4/80	8/40	10/94	12/45	64/402
Spathochlamys sp. A	2 g, h	—	—	—	—	2/11	—	1/2	1/1	—	4/14
Spathochlamys vestalis (Reeve, 1853)	2 e, f	20/82	20/85	—	—	—	—	—	—	—	40/167
Total Richness		11	8	17	14	21	15	17	16	14	33
Total Localities		42	35	18	13	27	16	30	27	22	230

Table 3

Measures of Diversity. Values are given for all 9 regions sampled in this study and combined as oceans for comparison. Richness is the number of species, H is the Shannon-Weiner Index, and α is Fisher's Alpha. H and α are calculated as described in the text.

Region	Rich-ness	H	α
All Caribbean Samples	22	2.1188	3.0477
Cochinos Cays, Honduras	17	2.0679	3.9760
Mosquito Cays, Nicaragua	15	1.4470	3.0575
Almirante Bay, Panama	15	1.9501	3.0989
Bocas del Toro, Panama	21	2.0257	3.8361
Chiriqui Lagoon, Panama	17	1.7113	3.0812
Gulf of Mosquitoes, Panama	16	1.5847	2.6138
San Blas, Panama	14	2.1150	3.3667
All Eastern Pacific Samples	11	1.4103	1.3840
Gulf of Chiriqui, Panama	11	1.3788	1.4340
Gulf of Panama, Panama	8	1.4303	1.2242

snorkeling in 2 meters water depth from the Bocas del Toro region of Panama, and therefore not included in analyses of the dredge samples. Numerous other specimens were observed living attached to branching corals

Table 4

Geminate species pairs. We are considering 9 groups of species to be geminate species pairs. All but 1 of these pairs includes a previously undescribed species. Undescribed species are indicated using open nomenclature as discussed in the text.

Pacific geminate	Caribbean geminate
Bractechlamys sp. H	*Bractechlamys antillarum*
Euvola sericeus	*Euvola* sp. E
Euvola perulus	*Euvola* sp. F
Leptopecten velero	*Leptopecten bavayi*
Leptopecten biolleyi	*Leptopecten* sp. C
Lindapecten sp. B	*Lindapecten acanthodes*
Nodipecten arthriticus	*Nodipecten* sp. G
Pseudamusium (Peplum) fasciculatum	*Pseudamusium (Peplum)* sp. D
Spathochlamys vestalis	*Spathochlamys* sp. A

and additional specimens have been identified from private collections in the region (Kim Hutsell, personal communication, 2001). Olsson and McGinty (1958) reported the species *C. mildredae* from Bocas del Toro, well outside its previously reported geographic range. Cahill (1990) discredited this report based on his inspection of several specimens from the San Blas Archipelago finding
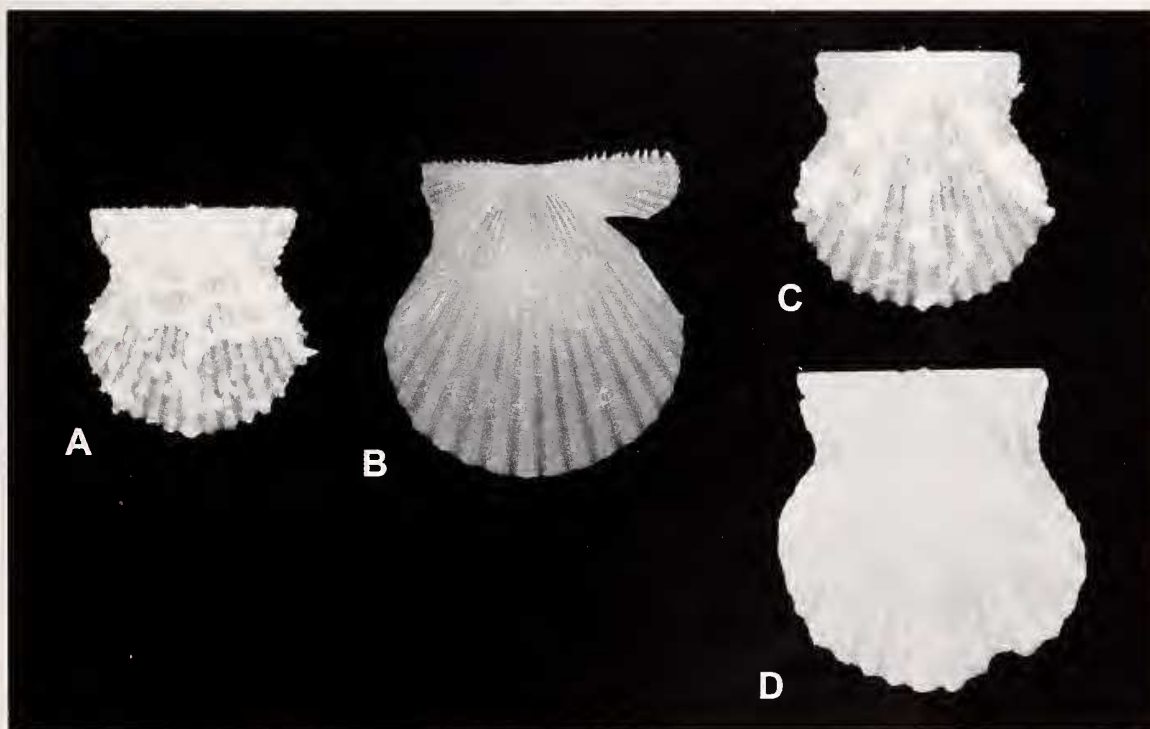

Figure 11.   *Lindapecten.* (A) *Lindapecten acanthodes* (CTPA 334-B-5, lvh = 4.92 mm), (B) *L. acanthodes* (CTPA 445-B-3, rvh = 13.88 mm), (C) *L.* sp. B (CTPA 394-B2, lvh = 5.16 mm), (D) *L.* sp. B (CTPA 399-B-147, lvh = 10.53 mm).
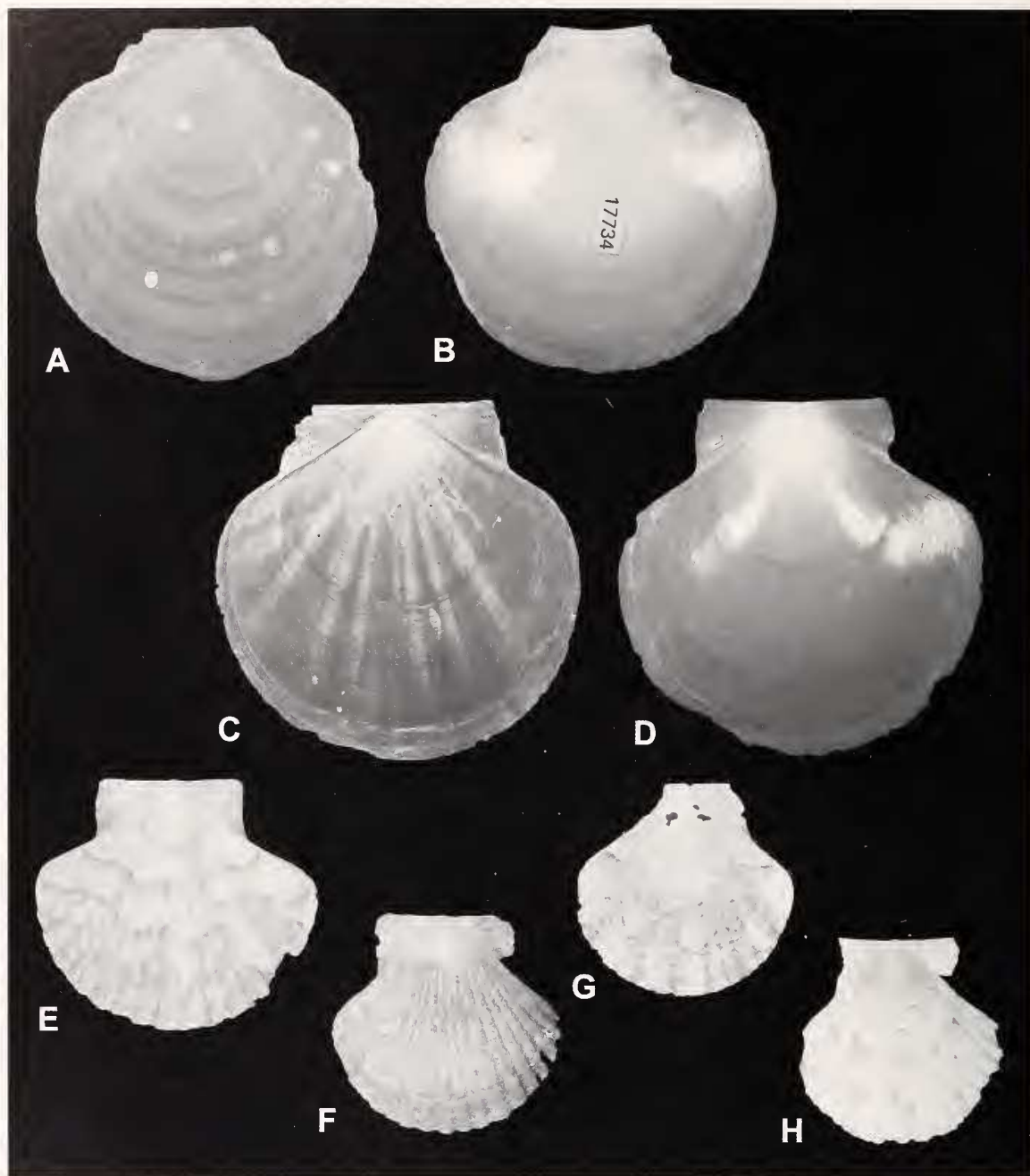
Figure 12. *Euvola.* (A, B) *Euvola marensis* (NMB G 17479, (A) left valve height (lvh) = 59.92 mm, (B) right valve height (rvh) = 57.91 mm), (C, D) *E. laurenti* (CTPA 494-B-11, (C) lvh = 61.31 mm, (D) rvh = 64.38), (E) *E. perulus* (CTPA 378-B-77, lvh = 21.33 mm). (F) *E. perulus* (CTPA 368-B-100, rvh = 28.71 mm), (G, H) *E.* sp. F (CTPA 534-B-62, (G) lvh = 17.38 mm, (H) rvh = 17.85 mm).

that these specimens were variants of *Caribachlamys imbricata* (Gmelin, 1791) and specimens of that variant were most likely the basis for Olsson and McGinty's report. However, our discovery indicates that Olsson and McGinty most likely did sample this species although it

may not be *C. mildredae.* It is apparently intermediate between *C. imbricata* and *C. mildredae.* Once again, extensive sampling is essential before one ascribes too much taxonomic importance to the absence of specimens from collections.
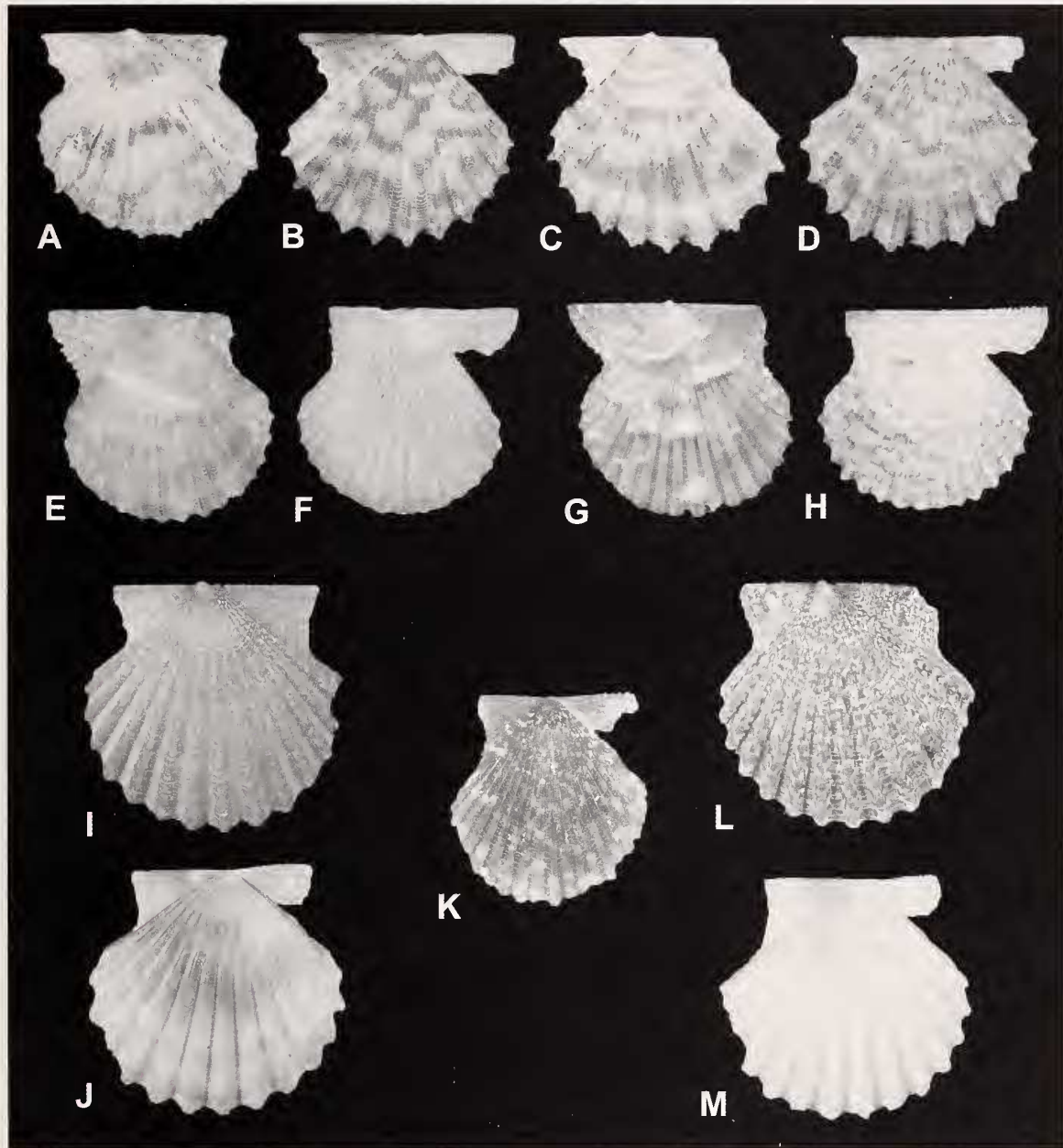
Figure 13. *Leptopecten* and *Pacipecten*. (A, B) *Leptopecten biolleyi* (CTPA 465-B-169, (A) lvh = 10.31 mm, (B) rvh = 8.72 mm), (C, D) *L.* sp. C (CTPA 485-B-111, (C) lvh = 10.06 mm, (D) rvh = 10.41 mm), (E, F) *L. velero* (CTPA 407-B-172, (E) lvh = 8.78, mm (F) rvh = 7.33 mm), (G, H) *L. bavayi* (CTPA 556-B-46, (G) lvh = 8.61 mm, (H) rvh = 8.49 mm), (I, J) *Pacipecten tumbezensis* (CTPA 421-B-67, (I) lvh = 20.62 mm, (J) rvh = 24.83 mm), (K) *P. leucophaeus* (CTPA 533-B-76, rvh = 7.52 mm), (L) *P. linki* (CTPA 337-B-49, lvh = 15.14 mm), (M) *P. linki* (CTPA 538-B-58, rvh = 15.34 mm).

CONCLUSIONS

The numbers of species of scallops in the southwestern Caribbean is more than double that in the tropical Eastern Pacific. However, the magnitude of differences observed across the Isthmus depends greatly on the frequency and spatial scale of sampling. Numbers of species from in-dividual large samples are similar in the two oceans be-cause the much greater abundance of specimens in the Pacific masks the actual differences in regional diversity. These differences are consistent with the much higher primary production by phytoplankton and greater food availability for suspension feeders in the tropical Eastern Pacific (Birkeland, 1977, 1987; Coates et al., 1996;
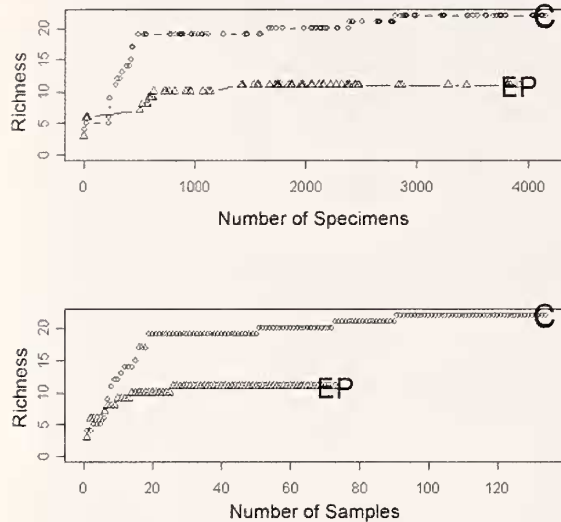
Figure 14. Species richness. Plots of species richness shown as cumulative sampling curves for both number of specimens (upper plot) and number of samples (lower plot). Diversity is plotted as species richness for the Caribbean (C) and the Eastern Pacific (EP).
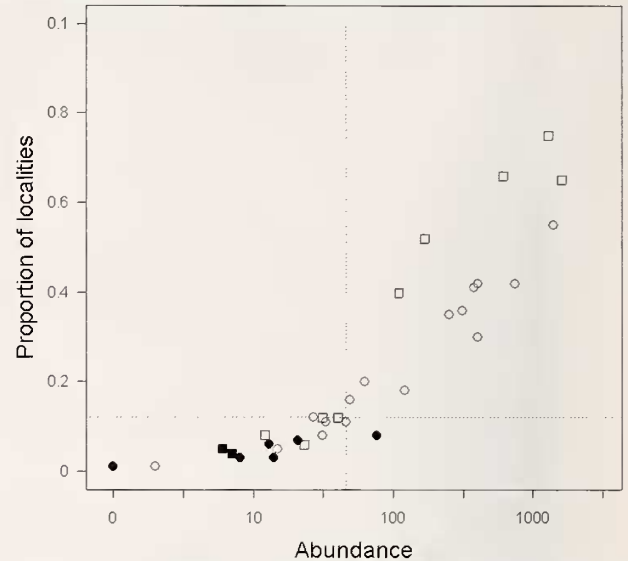

Figure 16. Abundance vs. geographic range. Pacific species represented by squares and the Caribbean fauna by circles. Previously undescribed species shown as solid points.

D'Croz and Robertson, 1997; Jackson & D'Croz, 1998). Numbers of species from the different regions sampled are consistently about one and one half times greater in the Caribbean regions compared to the Eastern Pacific, and even higher at Bocas del Toro. However, many Caribbean species occur in only a fraction of the regions sampled, as compared with the broader distribution of Eastern Pacific species. This is because of the much greater differences in environmental conditions such as

the relative abundance of well developed coral reefs and sea grass meadows among the Caribbean regions. Thus, the full differences in diversity are only apparent after intensive sampling from all the regions combined, and even this is almost certainly inadequate for collecting all the species present.

These effects of sampling scale are summarized in Figure 17, showing the relationship between numbers of species encountered and the geographic area (numbers of
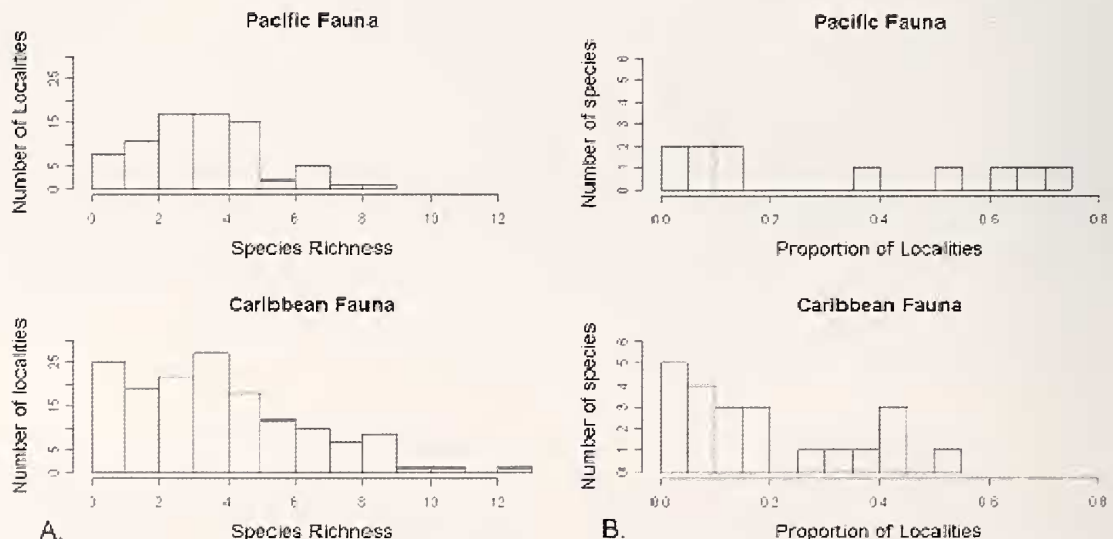

Figure 15. Commonness and abundance of tropical scallops. Upper plots represent the Pacific fauna and the lower plots the Caribbean. (A) Histogram of species richness by locality. (B) Histogram of proportion of localities of occurrence. Proportion is plotted as opposed to absolute numbers of localities to normalize for unequal sampling effort.
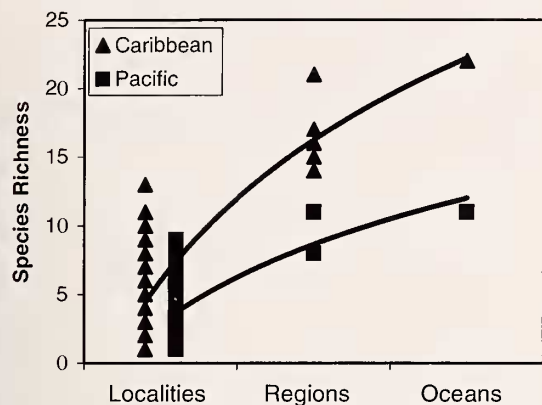
Figure 17. Species area plot. The x-axis represents 3 distinct "geographical" values: locality, region, and ocean. The y-axis plots the number of species found. Points do not depict the distribution of values, only the ranges. The lines were plotted as a simple best-fit model using Excel.

regions) sampled. The curves describe a general logarithmic fit to the data from each ocean in the form of sampling effort curve. Despite the larger number of regions sampled, the Caribbean curve is still rising steeply in comparison to the Eastern Pacific. In some ways this is analogous to Whitaker's (1972) measurement of beta diversity. The alpha (local) diversity is roughly the same in either ocean, which very likely explains the considerable previous confusion about patterns of diversity across the Isthmus. Beta (regional) diversity is more difficult to quantify, but in this analysis it can be crudely approximated as the slope of the line as the geographic range is expanded from locality to region to ocean. This slope is much higher in the Caribbean than in the Eastern Pacific. The gamma (ocean) diversity is clearly higher in the Caribbean, although considerably more sampling is needed in both the Eastern Pacific and southwest Caribbean to more accurately estimate the magnitude of difference across the Isthmus.

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